

## RESEARCH ARTICLE

# Relationships Between the Fossil Colobine *Mesopithecus pentelicus* and Extant Cercopithecoids, Based on Dental Metrics

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Maxillary dental measurements from six specimens of *Mesopithecus pentelicus*, 64 cercopithecines, 59 African colobines, and 64 Asian colobines were analyzed by means of a “nested research design” that was specifically designed to explore the affiliation between fossils and extant cercopithecoids at different systematic levels. The results showed that the variation among taxonomic groups was mainly associated with size; however, in addition, interesting shape differences emerged, molars were shown to be important discriminators, *Mesopithecus* was confirmed as a colobine (as expected) and found to be closer to Asian species than to African ones, and the odd-nosed colobines were found to share more dental similarities with *Mesopithecus* than other colobines. The last finding is in contrast to previous studies, in which it was proposed that *M. pentelicus* is morphologically closely related to the African colobus and the gray langur (*Semnopithecus*) in Am. J. Primatol. 62:287–299, 2004

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**Key words:** colobines; fossil (*Mesopithecus pentelicus*); metrical dental analysis on cercopithecoids; functional adaptation

## INTRODUCTION

Colobines (subfamily Colobinae) constitute one of the two subfamilies of Old World monkeys (the Cercopithecidae) that are found in Asia and Africa [Delson, 1994; Groves, 2001]. After their initial divergence in Africa, the ancestors of Eurasian species spread into Europe at about 10 Ma in the Middle Miocene. They were abundant there for a while, but eventually they declined and disappeared. A few groups spread eastward into Asia by the end of the Miocene or Early Pliocene [Andrews et al., 1996; Delson, 1994; Sterner et al., 2003; Stewart & Disotell,

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1998]. Because of the scarcity of fossils in Asia, the relationships between extinct species in Eurasia and extant colobines in Africa and Asia are still heatedly debated. The scenarios associated with dietary selection and functional adaptations of the fossil species are still unknown.

The earliest well-known fossil that is supposed to be closely related to the extant colobines is *Mesopithecus pentelicus*. This fossil was first found at Pikermi, Greece, and was dated at about 8.5–6 Ma. The genus *Mesopithecus* includes three species (*M. pentelicus*, *M. monspessulanus*, and *M. delsoni*), the fossils that are found in deposits from the Late Miocene to the Middle Pliocene in southern and central Europe, and southwest Asia, including the Indo-Pakistan Siwaliks [Andrews et al., 1996; Barry et al., 1987; de Donis et al., 1990; Delson, 1994; Gentili et al., 1998; Rook, 1999]. The relationship of this genus with modern colobines has been discussed for many years [e.g., Andrews et al., 1996; Delson, 1994; Szalay & Delson, 1979; Zapfe, 1991]. The postcranial features, size, and locomotor pattern of *Mesopithecus* have been considered to be comparable to those of the gray langur (*Semnopithecus*) of southern Asia [Andrews et al., 1996; Delson, 1994; Szalay & Delson, 1979; Zapfe, 1991]. *Mesopithecus* has also been considered to be related to other, smaller Asian colobines on the basis of cranial morphology [Delson, 1973] and the structure of enamel prisms [Dostal & Zapfe, 1986]. A recent cladistic study [Jablonski, 1998] allied it with the odd-nosed species (specifically, the douc langur (*Pygathrix*) and proboscis (*Nasalis*)), and proposed that they could be regarded as sister taxa. Contrary to these proposed Asian relationships, Strasser and Delson [1987] considered *Mesopithecus* to be close to African colobines because of the absence of the proximal cuboid-ectocuneiform facet. These affinities were supported by Hohenegger and Zapfe [1990] on the basis of cranial morphometric similarities.

In this study, we explore the affinities of *Mesopithecus* using dental metrical analyses. We also put forward a scenario for diet and functional adaptation.

## MATERIALS AND METHODS

Six specimens of *M. pentelicus* (three from Pikermi, Greece, and three of unknown origin) that were stored in the British Museum of Natural History, London, were measured. The measurements (the maximal mesiodistal lengths and buccolingual widths (taken perpendicular to length) from the first incisor (I1) to the third molar (M3) in maxilla (16 variables in all)) were obtained with digital calipers. The same measurements were also taken from extant Cercopithecoids. The specimens included 1) 59 African colobus (*Colobus guereza*, *Piliocolobus badius*, and *Procolobus verus*); 2) 64 individuals of Asian colobines, including snub-nosed monkeys (*Rhinopithecus roxellana*, *R. bieti*, *R. brelichi*, and *R. avunculus*), douc langur (*Pygathrix nemaeus* and *P. nigripes*), proboscis (*Nasalis larvatus*), pig-tailed langur (*Simias concolor*), gray langur (*Semnopithecus entellus* group), leaf-eating monkeys (*Trachypithecus phayrei*, *T. francoisi*, *T. cristatus*, *T. obscurus*, *T. vetulus*, *Presbytis rubicunda*, *P. comata*, and *P. melalophos*); and 3) 64 specimens from 16 cercopithecine species, including macaques (*Macaca nemestrina*, *M. nigra*, *M. silenus*, *M. thibetana*, *M. arctoides*, *M. assamensis*, *M. sinica*, *M. radiata*, *M. fascicularis*, *M. fuscata*, *M. mulatta*, and *M. sylvanus*), baboons (*Papio hamadryas* and *P. ursinus*), and drills (*Mandrillus leucophaeus*). There was an approximately equal number of males and females in each group.

We examined the data using principal-components analysis (PCA) and discriminant-function analysis (DFA). The former tests whether there is

significant variation among groups/species when all specimens are treated as a single data universe. The latter explores the variation between groups/species when each is regarded as an independent group on the basis of definitions external to the data.

Three consecutive sets of analyses were set up and constituted a “nested research design” that was specifically constructed to assess the relationships between fossil and extant species. First, the three groups defined above, together with the fossils, were examined separately by PCA and DFA. The purpose here was to detect the positions of the fossils in the first two axes of PCA and DFA, which occupy a major part of the total variation. This procedure allows one to select the group or groups at the generic level that show the closest relationships with the fossils. Second, each selected genus from the previous step was regarded as a group (individual species were not differentiated). The purpose here was to search for the genus/genera to which the fossil species was closest. Third, the species in that genus/genera were analyzed with the fossils, with each species regarded as a group. In this way, the extant species that displayed the closest relationship with the fossils were detected.

Thus, in addition to providing profiles that show different relationships between fossil and living species at these hierarchical taxonomic levels, this design sets up a logical means of searching for the extant species that show the closest relationship with the fossils. It avoids the weakness inherent in DFA when too many groups are analyzed (i.e., the precision of discrimination would be reduced if all 189 species were treated with the fossils in a single overall analysis).

## RESULTS

The eigenvalues and eigenvectors of PCA for the species studied are listed in Table I. The first two axes account for 86.79% of the total variation (82.79% and 4.0% for the first and second axes, respectively). Each variable in the first axis shows very high positive eigenvectors, indicating a high degree of size dependence. In the second axis, the canine (both length and width) makes the greatest positive contribution to the variation. Two other variables (P3MDL and I2BLL) display very low positive contributions. The rest of the variables demonstrate negative contributions. Thus, the second axis contains some shape-related variation because of the dichotomy (positive and negative) of the contributions, but accounts for only a small proportion (4.0%) of the total variance.

The dispersion of the three extant cercopithecoid groups and the fossils along the first two axes of the PCA is illustrated in Fig. 1. Most individuals of the cercopithecines lie on the right side of PC1; the colobines tend to be on the left, and the fossils overlap widely with the colobines.

The results from DFA, based on the same taxa analyzed in the PCA, are provided in Table II. The total variance explained by the first two axes is 98.0% (the first accounts for 76.3%, and the second for 21.7%). The widths of I1 and M2 have strong positive loadings on DF1, and the lengths of M2 and M3 are less strongly loaded, while M1 and M3 widths are very strongly negatively loaded. In the second axis, the width of M1 is very strongly positively loaded, and that of M3 is very strongly negative (both coefficients are  $>2.0$ ). Another variable with a relatively high positive loading score is the length of M3 on the same axis.

The segregation among groups revealed in the PCA is even more impressive in the DFA (Fig. 2). The divisions between the groups here are quite clear, with few overlaps. The colobines fall to the left of the diagram, which means they have narrow I1, short and narrow M2, broad M1, and short but broad M3 compared to

**TABLE I. Eigenvalues and Eigenvectors of the First Two axes of PCA Based on All Extant Specimens (*Cercopithecidae*) and the fossils**

	PC1	PC2
Eigenvalues	13.25	0.64
Percentage	82.79	4.00
Cumulative %	82.79	86.79
Eigenvector		
Length		
I1MDL	0.884	-0.057
I2MDL	0.871	-0.096
CMDL	0.799	0.557
P3MDL	0.906	0.009
P4MDL	0.948	-0.057
M1MDL	0.948	-0.069
M2MDL	0.962	-0.095
M3MDL	0.959	-0.085
Width		
I1BLL	0.895	-0.037
I2BLL	0.925	0.039
CBLL	0.830	0.494
P3BLL	0.851	-0.092
P4BLL	0.905	-0.083
M1BLL	0.937	-0.113
M2BLL	0.966	-0.097
M3BLL	0.951	-0.095

Mesiodistal length and buccolingual width of the teeth are represented by MDL and BLL, respectively.

the cercopithecines. Compared to African colobines, Asian colobines have higher scores on DF2, indicating that they have extremely broad M1 and somewhat longer but relatively narrower M3. The fossil specimens are closely clustered and overlap completely with Asian colobines. Thus, only the Asian colobines were analyzed by DFA along with the fossils in the second step.

The DFA results for the six genera of Asian colobines and the fossil specimens are shown in Table III. The total variance accounted for by the first two axes is 86.7% (73.7% and 13.0%, respectively). In the first function, the lengths of the two premolars, and the widths from I1 to P3, are weakly negative; the rest of the variables show positive coefficients. The contribution from P4BLL is very close to zero. With regard to the second function, the variables that display positive loading scores include the lengths of I2 and P3, and the widths from I1 to M1, separately. Other variables have negative coefficients.

The arrangement of the Asian colobines and the individual fossils in the first two axes is illustrated in Fig. 3. In axis 1, the six extant genera are noticeably well separated, although there are some overlaps between *Rhinopithecus* and *Nasalis*, and between *Trachypithecus* and *Presbytis*. The single specimen of *Simias* falls in the *Trachypithecus* cluster. The high placement of *Semnopithecus* on DF1 indicates that it has large molars and mesiodistally long I1 compared to the other teeth, and the low position of *Presbytis* indicates the opposite. *Pygathrix* and *Semnopithecus* are high on DF2, indicating large incisors, broad P4, and narrow M2. The fossils are clustered where the dispersions of proboscis (*Nasalis*), snub-nosed monkey (*Rhinopithecus*), and douc langur (*Pygathrix*) overlap.

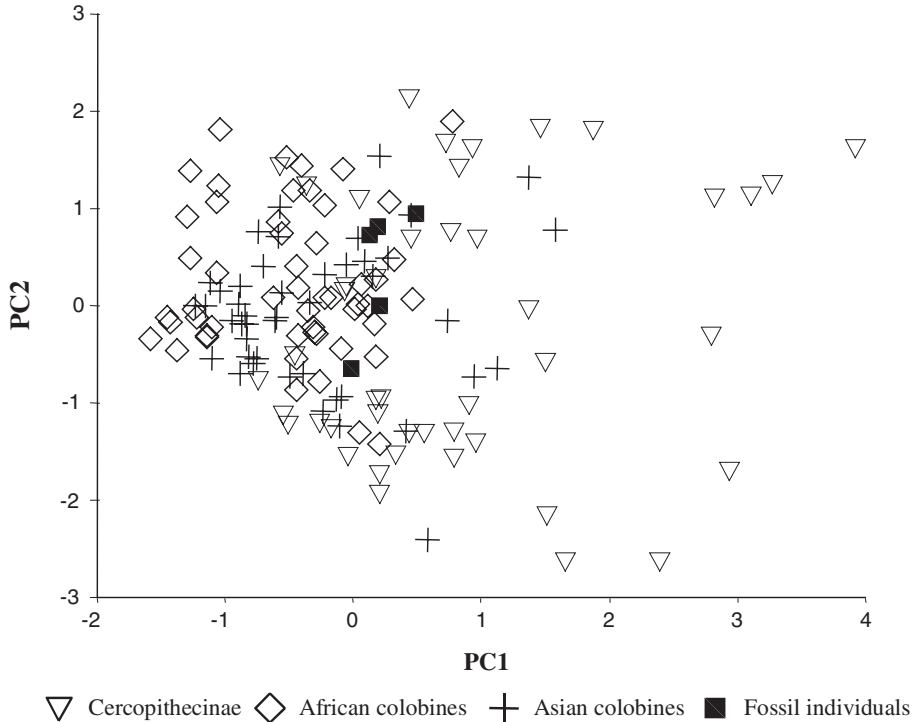


Fig. 1. Dispersion of the extant cercopithecoids and colobine fossil on the first two axes of PC1.

As a result of this step, the final analysis (DFA) included only the species of the odd-nosed monkeys and the fossils. The result of this examination indicates that 80.3% of the total variance is explained by the first two axes (66.1% and 14.2%, respectively; Table IV). In the first function, some variables (such as the lengths of P3 and P4, and the widths from I1 to P4 and M3BLL) show negative coefficients. Other variables display positive coefficients, in which M3MDL and M1BLL have the highest loadings. In the second function, the variables that show negative coefficients include the lengths of canine, P4, and M1, and the widths of I2 and M2. The rest of the variables show positive coefficients. However, two variables (CMDL and P4BLL) dominate the discriminant results in this function because of their very high values (negative and positive, respectively).

The dispersal profiles in Fig. 4 show that the two large *Rhinopithecus* species (*R. roxellana* and *R. bieti*) have overlapping distributions, while *R. brelichii* falls partly within and partly at the edge of the dispersal of *Nasalis*. *Simias* this time falls within *Pygathrix*. *Mesopithecus* falls in the region where *R. avunculus*, *R. brelichii*, and *Pygathrix* meet.

## DISCUSSION

The results of this study indicate that dental characters can play an important role in helping researchers to distinguish taxa at different systematic levels, explore the relationship between fossils and extant colobines and cercopithecines, and postulate profiles of functional adaptation in the fossils.

TABLE II. Eigenvalues and Standardized Canonical Coefficients in the First Two Axes of DFA Based on All Extant Species (*Cercopithecidae*) and the Fossils

	DF1	DF2
Eigenvalue	1.726	0.492
Percentage	76.3	21.7
Cumulative (%)	76.3	98.0
Canonical coefficient		
Length		
I1MDL	0.383	0.351
I2MDL	-0.263	-0.272
CMDL	0.039	-0.351
P3MDL	-0.250	-0.534
P4MDL	-0.118	-0.263
M1MDL	-0.498	0.157
M2MDL	0.811	-0.123
M3MDL	0.768	0.916
Width		
I1BLL	1.216	-0.277
I2BLL	-0.516	0.240
CBLL	-0.286	0.264
P3BLL	0.223	0.201
P4BLL	-0.121	0.109
M1BLL	-0.966	2.235
M2BLL	1.184	-0.365
M3BLL	-1.046	-2.266

Mesiodistal length and buccolingual width of the teeth are represented by MDL and BLL, respectively.

PCA shows that the dental measurements of cercopithecines are, overall, larger than those of colobines. This is perhaps not surprising when we consider that the species in the Cercopithecinae are generally larger in body size than species in the Colobinae, although there is wide overlap [Jungers, 1985; Napier & Napier, 1967]. *Mesopithecus* sort with the latter (Fig. 1). The canine dominates the variation in the second PCA axis, with highest loading scores for both length and width. This means that in addition to the differences in size revealed by PC1, cercopithecines and colobines show a noticeable difference in canine shape, expressed by the second axis. This may be associated with differences in patterns of canine sexual dimorphism, related to sexual selection, as shown by Plavcan [1993] (see also Plavcan and Van Schaik [1992]).

This separation between colobines and cercopithecines is even more marked in the DFA (Fig. 2). Molars are the most important discriminators, because both their lengths (M2 and M3) and widths (M1–M3) show large canonical coefficients on the first function, and the length of M3 and the widths of M1 and M3 demonstrate large coefficients on the second axis. This may be associated with dietary preferences. Although they show complex variations in certain aspects, the Cercopithecinae and Colobinae have been broadly regarded as frugivorous and folivorous, respectively, by a consensus of various authorities [Goldstein et al., 1978; Napier & Napier, 1967; Smith, 1983; Smith et al., 1983]. *Mesopithecus* resembles colobines, and this implies they may have the same diet.

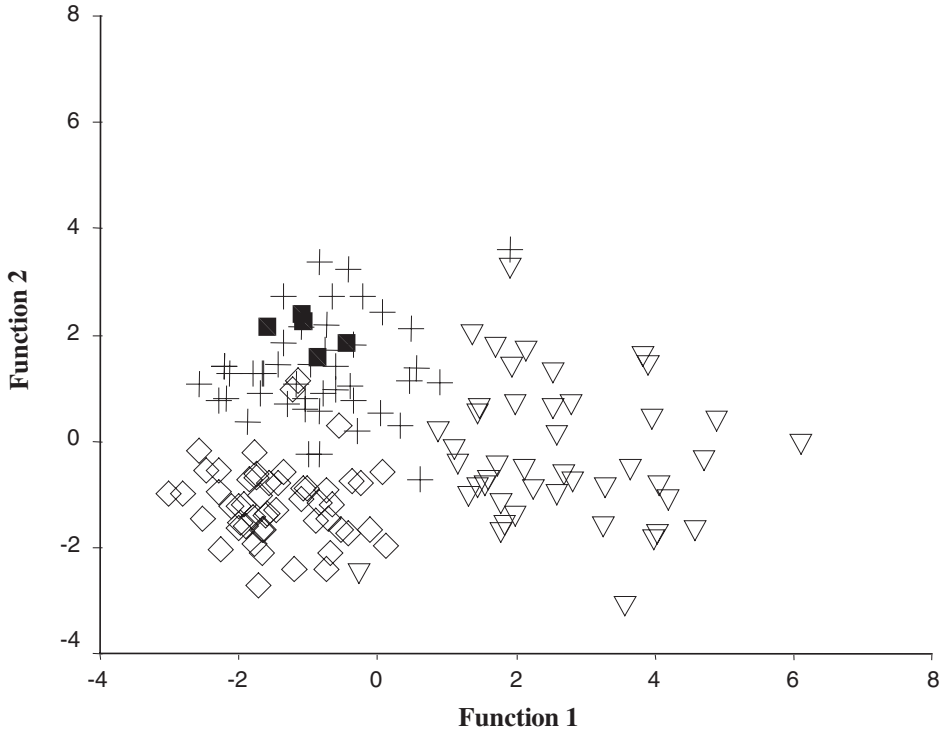


Fig. 2. Dispersion of the extant cercopithecoids and colobine fossil on the first two axes of DFA. (Symbols as in Fig. 1.)

Among the colobines, *Mesopithecus* is more closely related to the Asian representatives than to the Africans.

When analysis is restricted to Asian colobines, dental variation is reduced, especially regarding the first function (Tables II and III). That is, except for I2MDL, I2BLL, and P4BLL, which have very small canonical coefficients, the variable coefficients do not differ much, and only three widths (I1BLL, P4BLL, and M2BLL) dominate the discriminant results in the second function. Dental width, therefore, discriminates more effectively than length among the eight groups analyzed. The scatterplot indicates that *Mesopithecus* is close to *Rhinopithecus*, *Nasalis*, *Pygathrix*, and *Simias* (Fig. 3). This is in agreement with the cladistic studies of Jablonski [1998] and Byron [2001], who placed *M. pentelicus* as a sister group to a monophyletic clade containing the odd-nosed colobines. Rainforest leaf-monkeys (*Presbytis* and *Trachypithecus*) and human langurs (*Semnopithecus*) are located at the left and right sides in the same function, respectively. Thus, the profiles revealed here echo the taxonomic, phylogenetic, and evolutionary scenarios previously proposed for fossil and extant colobines, and for living Asian colobines specifically.

In the final analysis, width variables (such as CBL and M1BL in function 1, and CMDL, CBL, P4BL, and M2BL in function 2) have large canonical coefficients. Interestingly, the canine (both length and width) in the second function plays an important role, which implies that there may be significant canine differences among odd-nosed colobines. Further study on this issue is necessary. Figure 4 confirms the close relationship between *M. pentelicus* and the

**Table III. Eigenvalues and Standardized Canonical Coefficients in the First Two Axes of DFA Based on the Species of Asian Colobines and Fossil Individuals**

	DF1	DF2
Eigenvalue	9.370	1.659
Percentage	73.7	13.0
Cumulative (%)	73.7	86.7
Canonical coefficient		
Length		
I1MDL	0.170	-0.182
I2MDL	0.021	0.466
CMDL	0.114	-0.492
P3MDL	-0.106	0.178
P4MDL	-0.122	-0.008
M1MDL	0.219	-0.151
M2MDL	0.499	-0.115
M3MDL	0.345	-0.106
Width		
I1BLL	-0.143	0.594
I2BLL	-0.008	0.352
CBLL	-0.159	0.088
P3BLL	-0.174	0.034
P4BLL	0.003	0.944
M1BLL	0.235	0.066
M2BLL	0.161	-0.538
M3BLL	0.109	-0.182

Mesiodistal length and buccolingual width of the teeth are represented by MDL and BLL, respectively.

odd-nosed colobines that was revealed at the generic level, and the fossil shows a particular similarity with *Rhinopithecus brelichi*, *R. avunculus*, and *Nasalis larvatus* along the first function. These findings support the proposal to place *Mesopithecus* into a tribe (the Rhinopithecini) with the odd-nosed colobines [Groves, 2000], with the additional possibility that *Nasalis* should be included in the same tribe.

In this study, *Mesopithecus* showed no special similarity to *Semnopithecus*, in contrast to reports from Zapfe [1991] and Delson [1994] (see also Andrews et al. [1996]). *Semnopithecus* is noticeably separated from others in the present study (Figs. 3 and 4), and it also shows a unique pattern of sexual dimorphism compared to the other Asian colobines [Pan & Groves, 2004]. This could equally well indicate a wide phyletic separation or a more recent strong phonetic divergence.

Because of the very high correlation between tooth size and body size (the former is frequently used to predict the latter in fossil studies [e.g., Gould, 1975; Kay, 1975; Pilbeam & Gould, 1974]), the results of the initial PCA imply that the body size of *Mesopithecus pentelicus* is comparable to that of the odd-nosed species, and larger than that of the leaf-monkeys of the genera *Presbytis* and *Trachypithecus* [Sergio et al., 1998].

The colobines apparently underwent an early adaptive radiation in Europe. This is not unlike the ruminants, which immigrated to Europe (Pikermi-Samos) from Africa in the late Miocene. They diversified there and spread to Asia at the



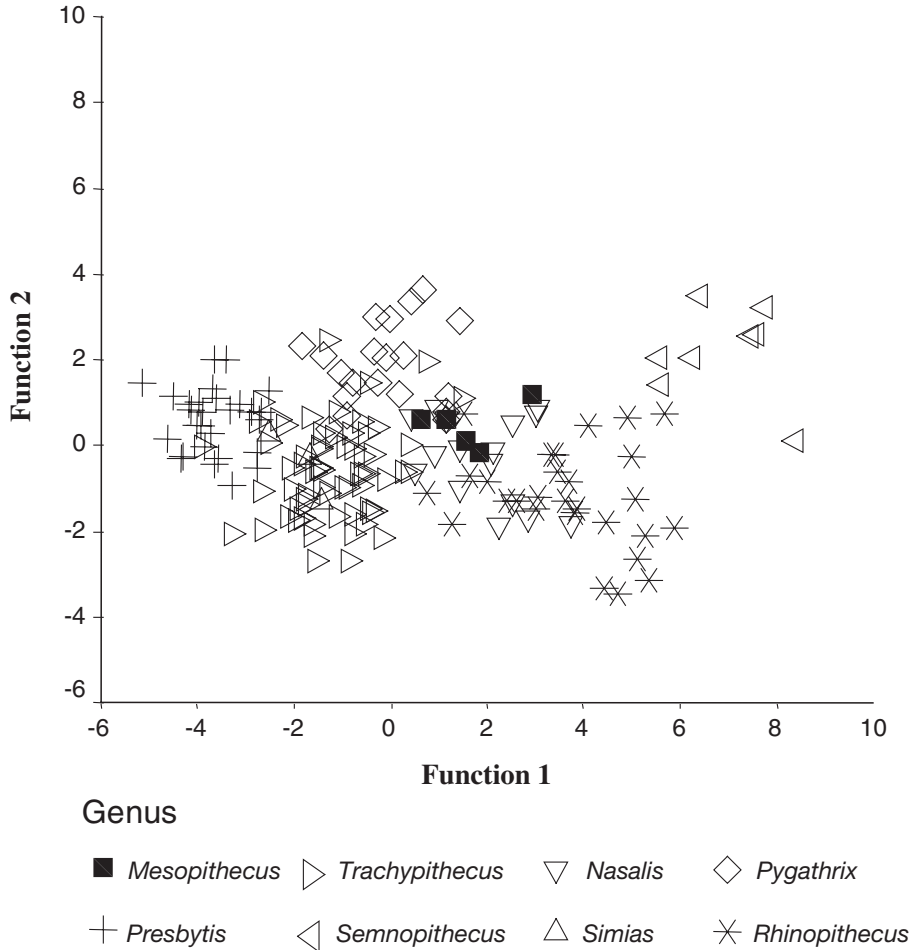


Fig. 3. Dispersion of the extant Asian colobines and the fossil species on the first two axes of DFA.

same time in the same forested and woodland environments. The descendants of the Pikermi-group ruminants are now found in Sichuan, southeast Asia, and India, where they occupy very similar niches as their ancestors [Solounias & Dawson-Saunders, 1988], and much the same seems to have occurred with the colobines. *Mesopithecus* was described as a relatively terrestrial form by Delson [1994] and Szalay and Delson [1979], and indeed some of the odd-nosed colobines are generally considered to be more terrestrial than other colobines (*Rhinopithecus*, very generally [Su et al., 1998; Peng et al., 1993; Pan & Jablonski, 1993; Wu, 1991], and *Simias* (which when disturbed, flees on the ground) [Wilson & Wilson, 1976; Tilson, 1977]; however, terrestrial locomotion is not reported for *Pygathrix* or *Nasalis*).

*Mesopithecus* is postulated to have followed a wooded savanna “corridor” into Europe. Most of the European colobines demonstrated terrestrial or cursorial locomotion, and their environment is described as woodland, and subtropical and temperate forests [Delson, 1994]. The paleoenvironment of *Mesopithecus pentelicus* in Pikermi and other European areas in the later Miocene (Turolian)

TABLE IV. Eigenvalues and Standardized Canonical Coefficients in the First Two Axes of DFA Based on the Species of Odd-Nosed Asian Colobines and Fossil Individuals

	DF1	DF2
Eigenvalue	11.550	2.476
Percentage	66.1	14.2
Cumulative (%)	66.1	80.3
Canonical coefficient		
Length		
I1MDL	0.232	0.335
I2MDL	0.239	0.331
CMDL	0.134	-1.189
P3MDL	-0.363	0.070
P4MDL	-0.305	-0.359
M1MDL	0.231	-0.386
M2MDL	0.385	0.053
M3MDL	0.700	0.074
Width		
I1BLL	-0.373	0.340
I2BLL	-0.050	-0.199
CBLL	-0.843	0.632
P3BLL	-0.184	0.136
P4BLL	-0.277	1.144
M1BLL	1.051	0.001
M2BLL	0.393	-0.665
M3BLL	-0.201	0.074

Mesiodistal length and buccolingual width of the teeth are represented by MDL and BLL, respectively.

was predominantly woodland, such as prevailed throughout Eurasia [Axelrod, 1975; Ioakim & Solounias, 1985; Leopold, 1969]. There was a high similarity to the present-day forests and woodland of Kanha in India, and fair similarity to other Asian regions, especially Sichuan (China). According to Jablonski [1998], the ancestral stock of the odd-nosed langurs would have occupied the woodland (broadleaf deciduous) and subtropical woodland (broadleaf evergreen) habitats that were widely spread from western through eastern Asia during the latest Miocene and early Pliocene.

These ecological niches were very similar to those in which the modern odd-nosed colobines adapted in east and (in part) southeast Asia, such as the conifer forests [Solounias & Dawson-Saunders, 1988] that are the main environment for Chinese snub-nosed monkeys in Sichuan (*R. roxellana*), the Qinghai-Tibet Plateau (*R. bieti*), and the Yuan-Gui Plateau (*R. brelichii*), which is adjacent to the Qinghai-Tibet Plateau [Pan & Oxnard, 2003]. Further south, the odd-nosed colobines have diverged more and more from this habitat, from *R. avunculus* in Vietnam to *Pygathrix*, *Nasalis*, and *Simias* in Laos, Cambodia, and southeast Asia (Borneo and the Mentawais), which are postulated to be derived from the northern forms [Pan & Oxnard, 2001]. They show a great variation in dietary preferences [Rowe, 1996], although in general there is a remarkable separation between the odd-nosed and the langur-like leaf-eating monkeys in their ecological niches (Groves, unpublished results) [Oates et al., 1994]. This implies that the diet of *Mesopithecus pentelicus* was more similar to those of the odd-nosed species

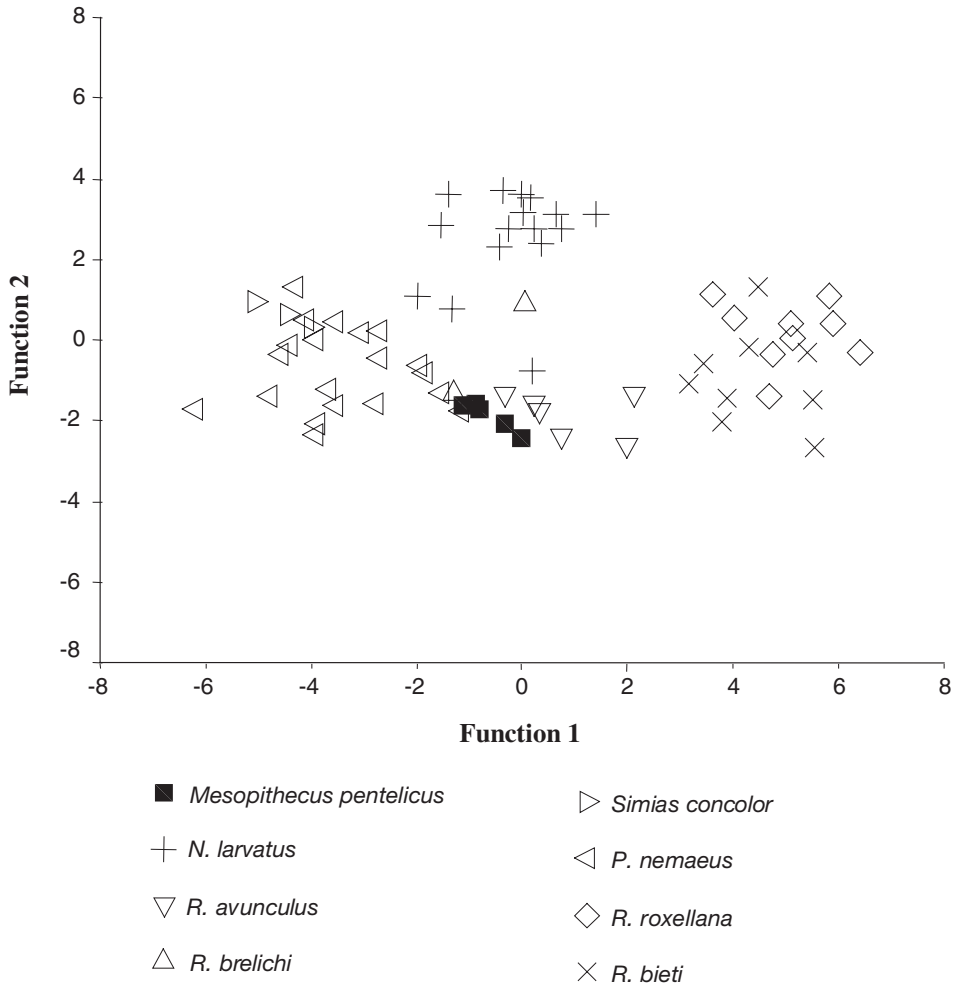


Fig. 4. Dispersion of the odd-nosed colobines and the fossil species on the first two axes of DFA.

(i.e., fruit, bark, leaf shoots, and flowers, and more mature than young leaves) than to those of *Presbytis* and *Trachypithecus*. Two recent studies based on dental microwear also suggested that *M. pentelicus* had a more frugivorous diet [Reitz & Benefit, 2001; Reitz, 2002].

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